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Spawning and Larval Development of the Trochid Gastropod *Calliostoma ligatum* (Gould, 1849)

by

ALAN R. HOLYOAK*

Department of Zoology, 574 WIDB, Brigham Young University, Provo, Utah 84602, U.S.A.

Abstract. Spawning and larval development through metamorphosis were observed in the trochid gastropod *Calliostoma ligatum*. Gametes were broadcast into the water column, sperm in white puffs and eggs in mucous strings. Larvae hatched as swimming veligers after 6 days, stayed in the water column for 3 to 4 days, and metamorphosed after 12 days. Broadcast spawning and planktic larvae indicate a more primitive reproductive strategy in *C. ligatum* than in other *Calliostoma* species which attach to substrata eggs from which hatch metamorphosed snails.

INTRODUCTION

Reproduction in *Calliostoma ligatum* (Gould, 1849), a common and conspicuous member of intertidal and subtidal communities along the Pacific coast of North America, has not been studied in detail. Information concerning the reproductive biology of this snail is limited to a brief report by HUNT (1980) on the eggs and their release. Developmental studies have been made on two other *Calliostoma* species: *C. zizyphinum* (Linnaeus) (LEBOUR, 1936; CROFTS, 1955) and *C. papillosum* (Da Costa) (ROBERT, 1902).

This paper presents a description of spawning and development through metamorphosis for *Calliostoma ligatum* collected in the San Juan Islands, Washington, U.S.A., in the winter and early spring of 1985. A comparison between the development of *C. ligatum* and other *Calliostoma* species is also made.

MATERIALS AND METHODS

Ten adults of *Calliostoma ligatum* were put in 800 mL of filtered seawater and placed in direct sunlight. When the water warmed, the snails began to release gametes.

Once spawning had commenced males and females were segregated by sex, rinsed to remove gametes, and put into 800 mL of 10–15°C filtered seawater. Both sexes continued to spawn after rinsing and transfer.

Eggs were pipetted from the bottom of the beaker and from the water column as they were released, transferred to 800 mL of fresh filtered seawater, and refrigerated until sperm were collected.

Sperm (3–5 mL) were collected as they were ejaculated and mixed with 100 mL of filtered seawater. This sperm solution was used immediately to fertilize previously collected eggs.

Approximately 100 eggs, or enough to nearly cover the bottom of a beaker, were pipetted into 800 mL of filtered seawater. Fertilization was accomplished by adding 2–3 mL of sperm solution to the eggs and gently agitating the gamete mixture for a few minutes. Fertilized eggs were rinsed to remove excess sperm. Beakers containing fertilized eggs were placed in a running seawater table and maintained at 7–9°C during development.

Cultures were periodically agitated, especially during early developmental stages. The water was changed each 2–3 h with freshly filtered seawater for the first day, and daily thereafter. No food was given to hatched larvae.

RESULTS

Spawning was first observed on 23 February 1985 with subsequent spawnings occurring through mid-April (Table 1). Spawning occurred during all lunar phases and included late morning and early evening hours. During all spawns the water temperature was at least 10°C.

Snails of both sexes moved to the air-water interface before releasing gametes.

Sperm were released as a milky white substance. No

* Current address: Institute of Marine Sciences, University of California, Santa Cruz, California 95064, U.S.A.

Table 1

Date, time of day, water temperature, and lunar phase during five spawnings of *Calliostoma ligatum*.

Date (1985)	Time	Water temp. (°C)	Lunar phase
23 Feb.	1700	10	New–1st Quarter
27 Feb.	1139	16	1st Quarter
1 Mar.	1815	11	1st Quarter–Full
9 Mar.	1915	10	Full
13 Apr.	1544	15	Last Quarter

size measurements of sperm were obtained. Cursory observations confirmed, however, that sperm were released individually and not in packets and that they were very active. Sperm release lasted 10–45 min.

Eggs were sheathed in mucous strands as they were spawned. These strands were 1–3 mm wide, held 1–4 eggs across the strand, and contained 10–90 eggs. Many pulses of eggs were released per spawn. Female spawns lasted 39–60 min and individual females released more than 1500 eggs. Eggs were not secured to any surface by adults but drifted to the bottom. The light green, granular eggs were opaque and 225 μm in diameter. The egg was separated from a gelatinous coat by a 20-μm wide space. The gelatinous coat was 30 μm in width and a frilly chorion 215 μm wide bordered that coat. An egg with its associated structures had a diameter of 750 μm (Figure 1A).

Fertilization and Development

Upon sperm penetration, the space between the egg and surrounding gelatinous coat increased from 20 to 50 μm and the gelatinous coat increased from 30 to nearly 100 μm in width (Figure 1B).

Development proceeded in a spiral cleavage pattern. The first two cleavages were meridional, equal, and holoblastic. The third cleavage was equatorial and unequal. Subsequent cleavages and differential cell divisions resulted in morula and then gastrula stages. For the timing of development see Table 2.

Gastrulae produced cilia at one end and ciliary beating caused spinning and rotation within the gelatinous coat. These cilia later formed the prototroch of the trochophore larvae (Figure 1C).

The shell gland and foot rudiment appeared during the trochophore stage. Shell secretion soon followed with the first sign of the larval shell being a shiny spot on one side of the trochophore. On the opposite side of the larva, the foot fold was becoming more prominent. Larvae soon thereafter became veligers (Figure 1D).

As prehatched veligers, larvae continued to secrete shell material and enlarge a now bilobate velum. The operculum formed during this stage, the digestive gland was visible,

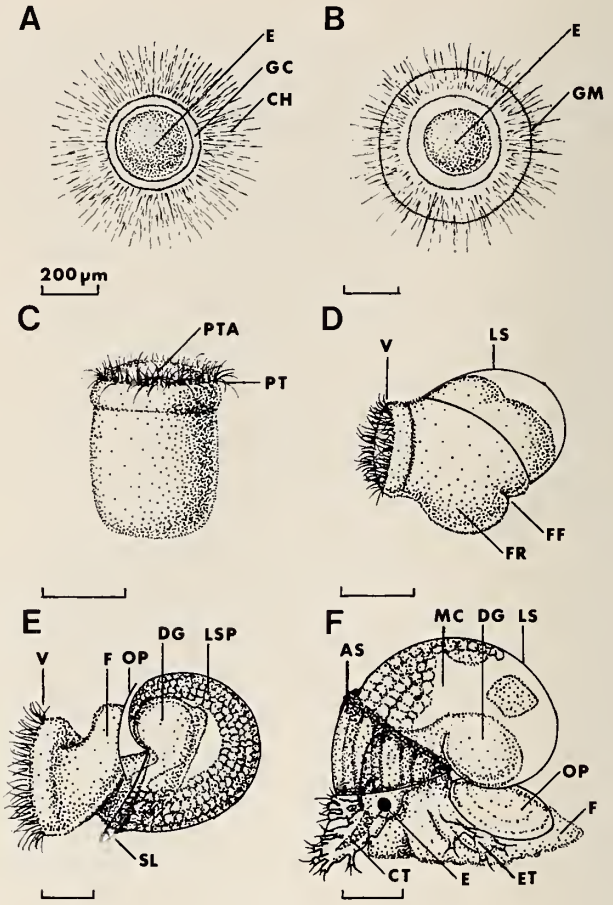

Figure 1

Developmental stages of *Calliostoma ligatum*. All scale bars represent 200 μm. A. Unfertilized egg: E, egg; GC, gelatinous coat; CH, chorion. B. Fertilized egg: E, egg; GM, gelatinous coat membrane. C. Trochophore: PTA, pretrochal area; PT, prototroch. D. Early veliger: V, velum; LS, larval shell; FF, foot fold; FR, foot rudiment. E. Prehatching veliger with torsion nearly completed: V, velum; F, foot; OP, operculum; DG, digestive gland; LSP, larval shell pattern (which covers the entire shell); SL, shell lip. F. Metamorphosed snail: AS, adult shell; MC, mantle cavity; DG, digestive gland; LS, larval shell; OP, operculum; F, foot; ET, epipodial tentacles; E, eyespot; CT, cephalic tentacle.

and larval shells had a honeycomb pattern and a lip. Torsion was also accomplished before hatching. At hatching the larval shell had 1¼ whorls (Figure 1E).

Calliostoma ligatum hatched as a swimming veliger after 6 days and spent 3–4 days in the water column. Individuals then went to the bottom where they spent 3–4 days crawling and swimming before metamorphosis occurred. During this swimming-crawling stage epipodial tentacles formed and the foot became mottled. At metamorphosis the velum was sloughed off, cephalic tentacles and eyes became readi-

Table 2

Timetable of the development of *Calliostoma ligatum*. Times are mean values for five cultures at 7–9°C.

Time	Stage
0 h	Fertilization
3.7 h	1st cleavage
5.8 h	2nd cleavage
7.4 h	3rd cleavage
1.8 day	Ciliated gastrula
2.1 day	Trochophore
2.4 day	Shell visible
2.6 day	Foot fold visible
3.1 day	Veliger
3.5 day	Shell pattern visible
4–5.5 day	Torsion
6 day	Hatching
9.5 day	Swimming-crawling
12.2 day	Metamorphosis

ly visible, and secretion of the adult shell was begun (Figure 1F).

Approximately 90% of fertilized eggs reached metamorphosis.

DISCUSSION

Spawning in *Calliostoma ligatum* depends on neither lunar phase nor on time of day since spawning occurred during all lunar phases and times of day as shown in Table 1. Elevated water temperature appears to be a primary factor in inducing spawning.

When *Calliostoma ligatum* spawns it broadcasts gametes into the water column. Broadcast spawning is unknown for other species within this genus. Two other *Calliostoma* species produce egg masses or at least attach an egg-bearing mucous string to the bottom (Robert, 1902; Lebour, 1937). *Calliostoma ligatum* falls between the spawning strategies of (1) eggs set free singly into the plankton, and (2) eggs laid in gelatinous layers (Purchon, 1977) by releasing eggs in a mucous string. In the laboratory, mucus integrity broke down and eggs were released into the water column. It is doubtful that developing larvae would be held in place by mucus in the field.

The eggs of *Calliostoma ligatum* obtained here are similar to those described by Hunt (1980) with the exception of egg size. Hunt reported eggs being 29–30 μm in diameter, certainly an error. Eggs in the present study were approximately 225 μm in diameter, a size comparable to egg sizes of *C. zizyphinum* (280 μm) and *C. papillosum* (170 μm) (Lebour, 1937).

The development of *Calliostoma ligatum* differs from other *Calliostoma* species that have been described. Other *Calliostoma* species bypass a planktic larval stage and hatch as metamorphosed snails (Lebour, 1937) while larvae of *C. ligatum* hatch as swimming veligers.

Swimming veligers of *Calliostoma ligatum* go to the bottom and swim and crawl for 3 to 4 days before metamorphosis. It is possible that the duration of the swimming-crawling stage would be shortened in the presence of a favorable substrate as has been suggested for other species (Scheltema, 1961; Fretter & Manly, 1977). The ability to prolong the swimming-crawling stage is advantageous as it allows larvae the time to search for favored habitats (Pechenik, 1980). Since clean glass is most likely not an ideal substrate, larvae in this study show that they will eventually metamorphose even if an ideal substrate is not present.

In conclusion, broadcasting gametes and hatching as planktic larvae places the developmental pattern of *Calliostoma ligatum* closer to the primitive gastropod pattern than that of other *Calliostoma* species whose development is known.

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